

ANT-VISITED EXTRAFLORAL (CALYX AND FOLIAR)
NECTARIES AND NECTAR SUGARS OF
ERYTHRINA FLABELLIFORMIS KEARNEY IN ARIZONA¹

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ABSTRACT

Extrafloral glands are noted on calyces of floral buds, before and during anthesis, and on petiolar stipels at early and later stages of leaf development. Liquid chromatographic sugar analysis of extrafloral and floral nectars shows that the extrafloral nectars (calyx and foliar) are fructose-glucose dominant while the floral nectar is sucrose dominant. Seven species of ants were noted visiting temporally separated calyx and foliar extrafloral nectaries, suggesting a possible myrmecophilous role.

Mattei's early (1925) report of extrafloral nectaries, to which he attributed a myrmecophilous role, on the calyces and leaf petioles of *Erythrina tomentosa* R. Brown ex A. Richard (= *E. abyssinica* Lamarck ex A. DC.; Krukoff & Barneby, 1974) and on the calyces of *E. hastifolia* Bertoloni (= *E. humeana* Sprengel; Krukoff & Barneby, 1974) has been overlooked in the literature on the genus. Apparently until recently no other species in this large and widespread tropical genus has been noted to have extrafloral nectaries or to be myrmecophilous. Feinsinger & Swarm (1978) note ant use of extrafloral nectaries on *E. poeppigiana* (Walpers) O. F. Cook and *E. fusca* Loureiro in Trinidad and Feinsinger et al. (this symposium) describe ant visitation of extrafloral-calyx glands on *E. fusca* and *E. pallida* Britton & Rose. Kearney (1894) made no mention of extrafloral nectaries in his description of *E. flabelliformis*. But in the since synonymized description of the same species from Baja California as *E. purpusi*, Brandegee (1903) described the calyx as "bearing a large gland on the lower lip."

Our study was initiated after preliminary observations during the summer of 1977 indicated that ants were visiting two types of extrafloral nectaries on *Erythrina flabelliformis* in southern Arizona. The purpose of this report is to describe the presence of calyx and foliar extrafloral nectaries on *E. flabelliformis*; to establish that the extrafloral nectaries produce sugars; to compare the relative proportions of glucose, fructose and sucrose in the extrafloral nectars and in the floral nectar; and to note the visitation of extrafloral nectaries by ants.

Raven (1974, 1977, this symposium) has reviewed knowledge on the biology

¹ James E. Ambrose, Jr. translated several points in Mattei's 1925 paper and gave permission to study *Erythrina* on his land, Ráfagas. Susan Kunz volunteered assistance in the field. James W. Berry and Charles W. Weber generously allowed J.C.S. use of their laboratory and equipment for the analysis of nectar sugars. Floyd G. Werner helped with preliminary identifications of ants. Roy R. Snelling, Los Angeles County Museum of Natural History, provided the final determinations of ant species utilized in the text. Charles H. Pickett, Peter Feinsinger, Herbert G. Baker, and Irene Baker provided us with copies of unpublished manuscripts. Herbert G. Baker and Jean L. Mills gave valuable criticisms of the manuscript. We thank all of the above for their contributions.

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of the genus *Erythrina* in introductory papers to the *Erythrina* symposia. It is a very distinct genus of Fabaceae consisting of 108 species of trees, shrubs, and a few herbs of wide distribution primarily in the tropics. Two species are native to the United States. *Erythrina flabelliformis* grows as a shrub on rocky outcrops in Arizona at the northern extent of its range (Conn, 1976); farther south in Mexico it attains tree form (Gentry, 1942). In Arizona *Erythrina* shrubs are dormant from fall until late spring. Kearney & Peebles (1960) note that the "flowers appear mainly in spring before the leaves" and Krukoff (1939) states that it is "aphyllous or rarely with young leaves at anthesis." Leafing appears to be in response to summer rains (Conn, 1976) and plants remain in leaf for approximately six weeks (Krukoff, 1939).

Narrow, tubularlike, hummingbird-pollinated flowers have evolved in New World species of *Erythrina* (Toledo, 1974; Raven, 1977) and *E. flabelliformis* is visited by hummingbirds in southern Arizona (Grant & Grant, 1968; Conn, 1976): including the black-chinned hummingbird, *Archilochus alexandri* (personal observation W.C.S.).

METHODS

Two Arizona populations, designated Molino Basin and Ráfagas, were utilized for this study. The first is located at 1,430 m elevation in Molino Canyon of the Santa Catalina Mountains (same population as studied by Conn, 1976). The second population is located in a box canyon (center of section 13, T17S, R23E, Pearce Quadrangle) approximately 1.6 km north of the entrance to Stronghold Canyon East at 1,520 m elevation in the Dragoon Mountains. During 1978 one or both of us visited Molino Basin twelve times and Ráfagas twice.

Ten shrubs were tagged at each locality and their locations were mapped to allow repeated collection throughout the season of various nectars (floral, extrafloral-calyx, and extrafloral-foliar) and ants from identified plants. Samples of floral nectar were easily obtained from all plants at both localities early in the season. Samples of extrafloral nectar were difficult to obtain as the quantities of nectar accumulated at the glands were small, usually not easily visible to the naked eye. Nevertheless, they were visited by ants (Figs. 1B, 1D). Only two plants provided sufficiently large samples of extrafloral-calyx nectar, and only one of extrafloral-foliar nectar, for collection and analysis. All three were Molino Basin plants.

Floral nectar was collected at Molino Basin on June 4 (3 plants) and June 18 (7 plants) and at Ráfagas on June 11 (10 plants). Extrafloral-calyx nectar was collected at Molino Basin on June 4 (3 plants; encrusted nectar) and June 18 (2 plants; clear, viscous fluid). Fifty additional plants at this locality were examined on June 22, but none contained sufficient quantities of extrafloral-calyx nectar for collection. In unsuccessful efforts to obtain samples of nectar from extrafloral-foliar nectaries, tagged plants at Molino Basin were visited eight times between July 16 and September 7; one sufficiently abundant extrafloral-foliar nectar sample was obtained at this locality on August 15 (1 plant; clear, viscous fluid).

Floral nectar was collected at anthesis from approximately 10 to 20 flowers as each was removed from an individual plant. The three samples collected on June 4 were obtained by breaking off the banner petal near its base and then lightly squeezing the calyx tube. This caused a nectar droplet to well up from the calyx tube at its upper lip near or between the wing petals. This nectar was taken up with a 50 μ l syringe, care being taken to avoid the region of the extrafloral gland on the lower lip of the calyx, and deposited in a vial with 80% ethanol. The pinkish, slightly-viscous nectar from these first three samples was later thought to be possibly contaminated by fluids from the ruptured banner petal. Subsequent samples of floral nectar (June 11, 18) were made in an identical manner except that the banner petal was plucked off at its natural juncture with the ovary wall. The resulting nectar droplet was clear in color, suggesting that earlier pinkish samples contained some petal fluids; June 4 samples were not included in the Molino Basin floral nectar analysis.

On June 4 extrafloral-calyx nectar that had apparently dried and become encrusted was removed from the orifices of glands on three plants and placed in 80% ethanol. This material failed to dissolve completely and when analyzed only two samples gave results of sugars. On June 18 two plants were found to have unusually large droplets of sticky, clear nectar balled-up on the surface of the extrafloral-calyx nectaries (Fig. 1A). This very viscous material was removed from buds of each plant by adhering it to the point of a syringe and then transferring it into 80% ethanol in collection vials where it dissolved readily.

On August 15 a sample of extrafloral-foliar nectar was collected in a similar manner from approximately 30 pairs of stipellate glands on leaf petioles of one plant. Ants had been excluded from selected branches of this and several other plants since August 2 by encircling the stem with VaselineTM petroleum jelly. (Ant exclusion seemed to facilitate the accumulation of nectar at extrafloral-foliar glands, Fig. 1C, but the technique did not increase the nectar accumulation on every plant so treated.)

On August 2 the position and number of extrafloral-foliar glands on the petioles of ten mature leaves of each of the ten tagged plants at Molino Basin were recorded.

All nectar samples were dissolved at the site in 80% ethanol, and later concentrated for chromatographic analyses by solvent evaporation in a nitrogen stream. Analyses were performed by direct injection of samples on a WatersTM model ALC/GPC 244 High Pressure Liquid Chromatograph equipped with a differential refractometer. Samples were eluted from a μ CarbohydrateTM (reverse phase) column under the following conditions: solvent—80:20 acetonitrile:water (isocratic elution); and flow rate—2.0 ml/min. The sugars were identified against standards by their retention times. Their relative concentrations were calculated by triangulation of peak areas and are reported as percentages of total sugars. (Note: standards of glucose, fructose and sucrose yield similar detector response versus concentration curves.)

It was beyond the scope of this study to relate chromatographic analyses to total sugar concentration within nectars. Total sugar concentration is subject to



FIGURE 1. Extrafloral (calyx and foliar) nectaries of *Erythrina flabelliformis*.—A. An unusually abundant concentration of clear, viscous droplets of extrafloral nectar on bud calyces.—B. *Camponotus ulcerosus* Wheeler (in circle) visiting an extrafloral-calyx nectary on an unopened floral bud (black arrows point to extrafloral calyx glands; white arrows point to emerging corollas of lower buds).—C. Extrafloral-foliar nectar concentrations (on ant-excluded plant) at openings in paired stipellate glands at the bases of secondary leaflets.—D. *Pseudomyrmex pallidus* F. Smith visiting one of a pair of extrafloral-foliar nectaries on an immature leaf (arrows point to enlarged glands on a younger leaf).

environmental changes, and its measurement requires large amounts of nectar collected under exacting conditions (Baker & Baker, 1975).

Samples of ant species found visiting either calyx or foliar extrafloral nectaries at both localities were collected during daylight hours and preserved in 80% ethanol. An effort was made to collect examples of all species foraging on each plant. Seven plants at Molino Basin were surveyed at least twice during the

season to determine if the same species of ants were visiting both calyx and foliar extrafloral nectaries of individual plants.

RESULTS AND DISCUSSION

In 1978 approximately half of the leafless plants at Molino Basin were in bloom on June 4, many of the remainder had developing inflorescences. By June 22 few floral buds remained, and on July 16 flowering had almost terminated and plants were developing leaves and seed pods. Later, on September 17, leaves were changing color. Thus the blooming period in 1978 was roughly one and a half months, and plants were in leaf during approximately the following two months. This phenological sequence agrees with the more detailed phenological data reported for the same site in 1975 by Conn (1976).

Two types of extrafloral nectaries were identified in *Erythrina flabelliformis*. An extrafloral-calyx nectary occurs on the lower lip, just below the corolla, of each grayish, pubescent calyx. This nectary is clearly evident on floral buds well before the scarlet red corolla appears, and the nectary remains obvious as a bright green, protruding, glandular structure throughout anthesis (Fig. 1B). The paired extrafloral-foliar nectaries are located on the ternate compound leaves on either side of the upper surface of the petiole, proximal to the attachment of the secondary leaflets (Fig. 1C). All 100 leaves surveyed had this pair of nectaries; three leaves had an additional pair on the petiole near the base of the terminal leaflet; and one had a single nectary in this position. Nectar is secreted via a horizontal orifice always located on the stem side of these modified, usually ovular, but sometimes pointed, stipels (Fig. 1C). Glabrous and green, these nectaries are clearly visible against the golden brown pubescence of immature leaves, only beginning to unfold their leaflets (Fig. 1D), and apparently they remain functional throughout the life of the leaf. Both types of extrafloral nectaries, calyx and foliar, resemble one another in size, color and surface texture.

The encrustations of nectar collected from the extrafloral-calyx nectaries of three plants failed to dissolve completely. Although the results of these analyses are therefore of questionable validity, two are recorded here: (1) glucose 75.7, fructose 15.0, sucrose 9.3; (2) glucose 87.9, fructose 12.1, sucrose trace. The two samples of clear, viscous nectar from the extrafloral-calyx nectaries dissolved completely and contained the following proportions of sugars: (1) glucose 42.8, fructose 47.3, sucrose 9.9; (2) glucose 41.4, fructose 50.5, sucrose 8.1. The single sample of extrafloral-foliar nectar contained the following proportions of the three sugars analyzed: glucose 54.2, fructose 45.8, sucrose trace. Thus it appears from these limited data that the proportions of the three major nectar sugars are similar in both types of extrafloral nectaries; sucrose is low in comparison to both glucose and fructose. Although differences in proportions of glucose and fructose in extrafloral-calyx and -foliar nectar may exist, these data are insufficient to evaluate that possibility.

Floral nectar of two populations of *Erythrina flabelliformis* was also analyzed. The Molino Basin sample (N = 7) contained the following proportions of the three sugars: glucose $\bar{x} = 14.9 \pm 1.7$; fructose $\bar{x} = 22.1 \pm 1.4$; sucrose $\bar{x} = 62.9$

± 2.7 . The Ráfagas sample ($N = 10$) contained the following: glucose $\bar{x} = 20.0 \pm 2.7$; fructose $\bar{x} = 21.3 \pm 2.4$; sucrose $\bar{x} = 58.7 \pm 4.9$. Sucrose is the dominant sugar in floral nectar and this contrasts with the situation in the two extrafloral nectars.

The nectars of *Erythrina flabelliformis* fall within two distinct types (dominant fructose and glucose; dominant sucrose) of three broadly classified types of angiosperm nectars identified by Percival (1961); the third type contains balanced amounts of sucrose, fructose, and glucose. Following comprehensive reviews of floral nectars, Wykes (1952b) and Percival (1961) concluded that the constituent sugars and their relative proportions tend to remain constant in a species, while their occurrence appears to be characteristic for certain families. Percival (1961) found long-tubed, leguminous flowers usually have sucrose dominant nectar. Baker & Baker (1980) confirm Percival's conclusions on within-family resemblances, but they note that the pollination biology of the species may influence the nectar type, even within taxonomic groupings.

Because of the possible presence of sucrose hydrolyzing enzymes, Bowden (1970) questioned the use of proportions of sucrose in nectars as a basis of classification, but Van Handel et al. (1972) felt that multiple sample consistency suggests the absence of the hydrolytic enzyme invertase, and they experimentally confirmed its absence in nectar of the century plant (*Agave sisalana*). Baker & Baker (1980) caution that in standing liquid nectar significant amounts of sucrose may break down due to natural nectar acidity or enzymes in the nectar (natural or introduced by micro-organisms). Quantitative variation in component sugars has been noted by Furgala et al. (1958) in the nectars of several legume crop plants and by Percival (1961) in 61 of 889 species studied. She (Percival, 1961) notes that although quantitative measurement may reveal that the nectar of all species varies within certain limits, these variations are not likely to alter their standing as to general nectar type.

Various authors have reported on the sugar constituents of extrafloral nectar (Percival, 1961; Baskin & Bliss, 1969; Bowden, 1970; Jeffrey et al., 1970; Butler et al., 1972; Elias et al., 1975; Keeler, 1977). A diversity of nectar types (sensu Percival, 1961) was found in various species, and both a correspondence and a lack of correspondence of nectar type was found between extrafloral and floral nectars of a species and between various extrafloral nectars, if present. Some plants have fructose-glucose dominant extrafloral nectar (Percival, 1961; Butler et al., 1972) as is reported here for *Erythrina flabelliformis*.

Percival (1961) reported associations between floral nectar type in some plants and the taxonomic group of the pollinators, but she noted that it is not known if differences in nectar composition (sugars) have any biological significance. Recently, Baker & Baker (1980) have argued that distinct types of nectar are characteristic of hummingbird-pollinated flowers (sucrose-rich), perching-bird-pollinated flowers (sucrose-poor), bat-pollinated flowers (sucrose-poor), nocturnal-moth-pollinated flowers (sucrose-rich), "true"-butterfly-pollinated flowers (sucrose-rich), and "bee-and-butterfly"-pollinated flowers (sucrose-poor). Baker & Baker (1975) have also noted correlations between several nonsugar constituents of nectar and classes of pollinators. Preferences for nectar type have

been investigated experimentally for two classes of flower visitors, honey bees (Wykes, 1952a; Waller, 1972) and hummingbirds (Hainsworth & Wolf, 1976; Stiles, 1976).

Evidence is accumulating which indicates that within the genus *Erythrina* species with sucrose-rich floral nectar are pollinated by hummingbirds and species with sucrose-poor floral nectar are pollinated by passerine birds (Cruden & Toledo, 1977; Baker & Baker, 1980, this symposium). Our results indicate that *E. flabelliformis* has floral nectar rich in sucrose. Thus, the proportions of sugars in the floral nectar of *E. flabelliformis* is in agreement with an apparent pattern found in the genus and amongst other hummingbird pollinated plants (Stiles, 1976; Cruden & Toledo, 1977; Baker & Baker, 1980).

The significance, if any, of differences in the proportions of the three dominant sugars in extrafloral and floral nectars of *Erythrina flabelliformis* is not apparent. Its understanding awaits definition of the roles and nectar preferences of associated fauna (hummingbirds, ants, nectar robbers, etc.), analysis of other nectar components, and/or other factors.

On June 11 five species of ants were noted visiting extrafloral-calyx nectaries of the 10 tagged plants at Ráfagas (numbers in parentheses indicate numbers of plants on which a species occurred): *Pseudomyrmex pallidus* F. Smith (1), *Crematogaster punctulata* Emery (8), *Forelius pruinosus* (Roger) (2), *Paratrechina* sp. (6), and *Camponotus ulcerosus* Wheeler (1). (Note: *Forelius pruinosus* has previously been in the genus *Iridomyrmex*.) Single plants harbored as many as three species. On June 4 and 18, 10 tagged plants at Molino Basin were also examined for ants visiting extrafloral-calyx nectaries. The five species encountered at Ráfagas were recorded here also (each species respectively on one, two, four, two and one plants) as well as two additional species, *Monomorium minimum* (Buckley) (1) and *Camponotus ocreatus* Emery (1). Two species of ants occurred on four plants; no ants were present on one of the plants; *Pseudomyrmex pallidus* were visiting corolla-damaged flowers on one plant. At Molino Basin on June 22 numerous *Crematogaster punctulata* were "robbing" floral nectar from an untagged plant.

The extended presence of *Crematogaster punctulata* at exposed floral nectaries of damaged flowers demonstrates acceptance of floral nectar by the ants, and suggests that factors other than ant-repellent characteristics of floral nectar chemistry (Janzen, 1977; Baker & Baker, 1978), such as morphological barriers in flower structure (Feinsinger & Swarm, 1978; Schubart & Anderson, 1978), are responsible for excluding some or all ants from floral nectaries of *Erythrina flabelliformis*.

Ants were observed at the extrafloral-foliar nectaries of eight of the tagged Molino Basin plants on August 5, 9, and 15. Five species of ants were seen visiting nectaries: *Pseudomyrmex pallidus* (3), *Monomorium minimum* (1), *Crematogaster punctulata* (4), *Forelius pruinosus* (3), and *Camponotus ulcerosus* (2).

Ants were seen visiting extrafloral nectaries on the calyces of floral buds during several stages of development: before the corolla appeared, while it was elongating and during anthesis (Fig. 1B). Throughout various periods of the

study ants were seen visiting foliar nectaries on juvenile leaves which had not unfurled their leaflets, and later, on fully developed leaves. Ants wandered over the inflorescences, stems, and/or leaves stopping briefly at the orifice of extrafloral nectaries (Figs. 1B, 1D), apparently to ingest small quantities of nectar, after which they would proceed to another extrafloral nectary. At Molino Basin, four of the five species of ants found on foliar nectaries had earlier been observed at calyx extrafloral nectaries of the same tagged plants. These observations suggest that on most plants the extrafloral nectaries, which are present from early in the initiation of flowering through leaf senescence, are visited by one or several species of ants throughout the flowering-leafing season.

The ecological role of ant visitation of extrafloral nectaries has received repeated attention over the years (Bequaert, 1922; Bailey, 1922; Wheeler, 1942; Bentley, 1977b). Recent studies in both tropical and temperate regions support the contention that a symbiotic, coevolved relationship exists between certain plants having extrafloral nectaries and the ants visiting them (Janzen, 1966, 1967; Hocking, 1975; Elias & Gelband, 1975; Bentley, 1976, 1977a; Tilman, 1978; Inouye & Taylor, 1979; Pickett & Clark, 1979). Feinsinger et al. (this symposium) recently reported that in three tropical species of *Erythrina* "inflorescences are protected by means of extrafloral [calyx] nectaries, which function to attract pugnacious ants."

Possibly one or more species of ants visiting extrafloral nectaries on *Erythrina flabelliformis* serve(s) a protective role in the ecology of the plant. If this proves to be the case, we speculate that the temporal phenological sequence of flowering season extrafloral-calyx glands followed by leafing period extrafloral-foliar glands may be adaptive for a seasonally extended myrmecophilous role.

The alkaloid-containing seeds of *Erythrina flabelliformis* (Hargreaves et al., 1974), although having a curarelike action (Folkers & Unna, 1939), suffer seed predation by larvae of a lepidopteran in Arizona (Raven, 1974; personal observations W.C.S.). Possibly, ants play a role in reducing seed predation by moth larvae. Such a seed-defense system in *E. flabelliformis* would combine (1) chemical deterrents incorporated within seeds with (2) seed-predator protection resulting from an ant-plant symbiosis fostered by extrafloral nectaries.

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